

agents, but it really was a rigid, scientific method which gave us our present knowledge of these diseases. The valuable results of the work on cereal smut infection furnish a fine example of achievement in disease-prevention that could not have been attained without both basic knowledge in mycology and a technique enabling trustworthy experimentation.

Upon entering a new biological territory, the first work is to collect and to classify, to know the material. So in the new field of plant pathology much of the early work was descriptive. The number of important plant diseases that are reasonably well described in two volumes of the Report of the United States Department of Agriculture for the years 1887 and 1888 is remarkable.

While the descriptive period in plant pathology is not entirely past, trivial diseases of cultivated plants, weeds, and wild plants still remaining undescribed, there have been very few really important diseases of general interest recently discovered in this country, few which compare in importance with the apple bitter rot, tomato leaf spot, onion smut, potato blight and scab, the cereal rusts or smuts. Many of the diseases recently described are of minor importance or are at present of very narrow geographic range; some have never been noted except by those who described them.

With the general principles of treatment established and the field for discovery of new diseases dwindling in importance, the time has now come when further progress, with rare exception, must be the outcome of fundamental, special knowledge and crucial experiments. It is evident that the easy crop from the virgin soil has been harvested, and that now we are entering upon the era of intensive cultivation.

The conquests of the future will be mainly the result of intensive study of the diseases and disease agents now known. Compare the degree of thoroughness of our knowledge of any one plant disease with any one disease in medicine. For example, compare from the research viewpoint our knowledge of *Pseudomonas campestris* with that of *Bacillus typhosis*; of the morbid histology of wheat rust with that of diphtheria; of the "epidemiology" of any plant disease with that of any human disease. Of course, the

parallel is not fair, since the values are not commensurate, but it serves to make the point that if such knowledge in medicine is probably contributory to prevention, probably it is also contributory in our science.

Thoroughness such as is attained in human pathology is in reality manifestly impossible for several reasons, one being the large number of plant diseases. Each plant species, to an extent, has its own fungous parasites; there are more than 40 listed for the apple alone. There are, perhaps, between 300 and 400 really significant, economic plant diseases, and to master knowledge of these is a great undertaking which is far from realization as yet.

Parasitic diseases present two chief elements, the host plant and the parasite. There is also, what is perhaps more important, the interrelation between these two, and what is also very important, the relation between these two and the factors of environment. It is with the study of these 5 elementary factors that pathology has to do. Large attention in the past has been given to the parasite, and in many cases it is the parasite alone which has been studied. Proportionately little study has been given to the relations existing between the host and the parasite, while the relations existing between environment and host, and environment and parasite, unquestionably of great significance, present a comparatively unworked field.

I wish to call attention briefly to the types of problems that exist under the above analysis. Perfecting and stabilizing of the taxonomy and nomenclature of the parasites are of course of fundamental value to pathology. The limitation of the families and orders of the fungi is, in the main, confessedly artificial; the boundaries of the genera are poor, and within the genera but little is really satisfying. To illustrate, the form genera *Penicillium* and *Coremium* are separated by ordinal rank, yet a single culture, dependent upon conditions, may give the characters of one or the other. Ordinal questions occur regarding *Meliola*, *Thielavia*, *Fusarium*, *Actinonema*, *Helminthosporium*, and many other genera.

Examples of problems in generic limitation are the *Phoma-Phyllosticta*, the *Septoria-Rhabdospora-Cylindrosporium*, the *Meliola-Capnodium-Apiosporium-Antennaria* questions. Within the

genus a good example is *Septoria* with 1200 species, or *Phyllosticta* with 1150 species. The former has nearly 700 species between 20 and 50 μ in spore length. The latter has 128 species with spores measuring 5–6 μ long. *Septoria* has 115 species on Compositae, and 77 species on the Gramineae (26 of these are within the limits of 20–40 μ in spore length).

Our present knowledge of such genera, as given by SACCARDO, is essentially that of a preliminary cataloguing of these forms by their hosts, the necessary first step. And we may add, as examples, the species of such genera as *Phoma*, *Rhabdospora*, *Cercospora*, *Nectria*, *Sclerotinia*, *Guignardia*, *Physalospora*, and *Phyllachora*. The bearing of this condition upon practice is evident, since numerous forms described as separate species upon the same economic host plant in reality may be identical or may be co-specific with forms described as distinct species or as belonging to other genera, families, or orders on the same or other hosts. The next step, well exemplified by such work as the monographs of THEISSEN, will consist in morphological comparison and readjustment of the species. This raises the question of life histories, of course, and shows the need of much such work as that of SHEAR and WOOD on *Glomerella*, HIGGINS on *Cylindrosporium* (*Coccomyces*), CLINTON on *Venturia*, WOLF on rose black spot (*Diplocarpon*), etc.

In connection with these problems arises the question of host relation and of biological specialization, as best exemplified, perhaps, in the rusts and the powdery mildews. What is the status of such specialization in the Fungi Imperfecti, in *Phyllosticta*, *Septoria*, *Cercospora*, etc., in the Ascomycetes, *Nectria*, *Sclerotinia*, *Phyllachora*, and many other genera? This forms a large and enticing field, in which much good work has been done, but a vast amount remains still to be done.

Coupled with these problems, come of necessity physiological, morphological, and cytological studies. The *Oospora-Actinomyces-Streptothrix* problem will require, apparently, all the possible side-lights before solution. This illustrates admirably the dependence of practice upon science, since fundamental questions of practice must rest their answer upon the degree of biological specialization

and variation of this organism, which causes potato scab, and concerning which we cannot decide as yet whether it belongs to the Eumycetes or to the bacteria.

Morbid histology of the various diseases presents a large field for activity. Concerning many diseases our knowledge in this regard is as yet really nil. It may be in many cases that such knowledge will not affect practice, but in many cases it surely has done so. Its utility appears clearly in relation to cereal smuts, tree surgery, etc.

The whole question of disease-resistance and susceptibility is fundamental and practical, as the age incidence of disease; the causes of resistance, whether mechanical, chemical, or physiological; the factors of air, soil, or heredity causing variation in resistance, and the possibility of artificially changing these factors. Breeding for disease-resistance is a special problem of extreme importance, involving knowledge of the factors of resistance and susceptibility, the needs of cultural conditions, and laws of breeding. Notable progress has been made with many crop plants, as oats, cabbage, asparagus, cantaloupes, carnations, flax, melons, and cowpeas.

Hibernation of the parasite has been the subject of much study. In some cases it offers the key to prophylaxis. It is, of course, inseparably linked in many cases with life history studies, and seems also sadly in need of study by those with sound ecological training. Indeed, an ecological study of certain plant parasites, with analysis of the environmental factors and with environments under experimental control, touching also upon seasonal relations, should be very productive. Problems abound on the border fields between mycology, physiology, ecology, and pathology relating to the age relation to disease, to mode of infection, to the climatic and seasonal relations of the parasite, to increase and decrease of susceptibility with changes of environment, to the results of varying the mass of the inoculum, and to change of the virulence of the pathogen with environment.

Epidemiology (to borrow the term from medical usage) is clearly linked with these topics. There is a vast amount of uncorrelated information in the literature concerning the relation between temperature, rainfall, etc., and various diseases, but there is ample

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room for a complete "epidemiological" study of any one of many really serious diseases.

A large field involving knowledge of extreme value and demanding ingenuity of experiment is that of pathogen transference. We know a little about transference by insects, but very little about wind and other agents.

Fungicides and their action are in need of more study. It is remarkable if accident has really given us the best fungicides in copper sulphate and lime sulphur. Our knowledge of their action and of their composition can be increased; so, too, the time to apply them and the strength to use. The exact time of application is undoubtedly of much importance; in some diseases, notably apple rust, the variable results are presumably linked with the time relation. Exact knowledge of such relation is needed in many cases. The subject of fungicide injury to fruits or foliage also arises here.

There are many diseases which have been described in a preliminary way, the causes of which are not yet known. Some of these are of great injury, notably the various so-called "mosaics," peach yellows and rosette. Their list is essentially included in the compilation of LANTZ (Ill. Agric. Exp. Sta., Circ. no. 183). It is not too much to hope that some of these will give up their secret under proper attack; some seem to have done so recently; for example, beet curly-top and the crown-gall. The status of others, such as Jonathan spot, tomato blossom-end-rot, tobacco mosaic, and numerous other mosaics, is not so clear. There is here opportunity for good descriptive work that we may know definitely with what conditions we have to deal. When the anatomical, histological relations are definitely recorded, we shall at least be able to classify these various types, and to know, for example, whether in reality the various things that we now call mosaic are of similar or different nature. Abnormal enzyme relations have been invoked to explain some disease conditions, but in general such explanations lack conclusiveness, and certainly lack practical application.

In these remarks I have not aimed at completeness. I have desired rather to indicate the need of intensive, thorough study of the problems before us, and to give a suggestive general view

of the field and of the diversity of research material. It is evident that no one person, either by temperament, inclination, or equipment, is fitted to investigate in all of these fields. The range is broad, and with a veritable wealth of research material, and a survey of the past shows that the well worked subject often is just as productive of results as an apparently much fresher subject. For years the powdery mildews have been introductory subjects in mycology. The group has been thoroughly monographed, collected, listed, years devoted to their biological specialization, treatments devised, etc. The field appeared too thoroughly worked to be promising of large results; yet recent studies have revealed the bud-scale hibernation habit of certain of these, and thus added fundamental knowledge useful in prophylaxis.

Finally, the diseases themselves, not the fungi, need classification. Various classifications have been used, as to cause, as to host, etc., but these do not serve to emphasize relationships of conditions which it is of service to know.

Aside from the non-parasitic diseases, those caused by improper environment of soil, air, light, by abnormal hereditary tendencies, by unknown factors and by predatory animals (including insects), and considering only those known to be caused by parasitic fungi, there are certain groups of conditions which stand out strongly marked as being similar. It is of distinct advantage in studying, in teaching, and in devising and promulgating remedies, to recognize and define these categories. By their very similarity, certain diseases have gravitated together; for example, the vascular diseases, fungous or bacterial diseases, with plugging of the bundles, popularly and very properly call the "wilts."

It is interesting to note that one of the most significant contributions along this line appeared in one of our elementary texts; significant, too, that this contribution should come from one not primarily interested in pathology. COULTER, in his *Elementary studies in botany*, gives us the conception of three general categories of plant diseases: (1) those in which the parasites kill the living cells; as pear blight, spot diseases, downy mildew, potato blight; (2) those in which the parasite does not kill the living cells, but lives in association with them, feeding upon their products; as rust, crown-gall, curl, black knot; (3) those in which the parasites

invade the vessels and live in the sap; as cabbage, cucurbit, and mushroom wilts and wood rot.

I have given some thought to this subject, and, as the only part of this paper which may lay any claim to originality, would present the following suggestions as a step toward a classification of plant diseases caused by fungi, separating them into the following categories:

1. Wilt diseases due to mechanical stoppage of the vascular bundles by parasites. These may be called cases of *embolism*; for example, vascular diseases due to *Ps. campestris*, *B. solanacearum*, and *Acrostilagmus*.

2. Disintegration of the xylem structures; for example, the various wood rots due to *Thelephora*, *Hydnum*, *Poria*, *Polyporus*, *Fomes*, *Trametes*, *Dedalea*, *Schizophyllum*, etc.

3. Diseases due to parasites wholly contained within the living protoplasm of the host cell. This is the strictest type of parasitism, and may appropriately be known as *endocellular parasitism*; for example, diseases due to *Synchytrium*.

4. Diseases due to parasites which draw their nutriment from living cells by haustoria, which may be called *endocellular haustorial parasitism*; for example, diseases due to *Phyllactinia*, *Peronospora*, *Albugo*, and *Plasmopara*. In this group the conspicuous feature is the relatively large development of the haustorial surface as compared with the remainder of the internal mycelium.

5. Diseases in which the live epidermal cells only are directly parasitized. These may be called cases of *epidermitis*, for example, diseases due to the Erysiphales (exclusive of *Phyllactinia*), *Meliola*.

6. Diseases in which the parasite grows between the living host cells. Haustoria may be present, but if so they are not prominent, and the apparently dominant part of the absorptive system is the intercellular mycelium. This may be called *intercellular mycosis*; for example, rusts, Exoascales, Exobasidiales, and *Cephaleurus*.

7. Diseases in which the host tissue is displaced or replaced by fungous masses. This may be called *mycosclerosis*; for example, diseases caused by *Claviceps*, *Phyllachora*, *Rhynisma*, and the smuts.

8. Diseases of the type produced by *Pseudomonas tumefaciens*, which may be called *tumor*.

9. Diseases in which the dominant feature is death of the host cells before they are actually invaded by the parasite. To these may be applied the term *necrosis*. Subdivision may be made on the basis of the part involved, as:

9a. *Cortical necrosis*, in which the cortex chiefly is involved; for example, cankers caused by *Sphaeropsis*, *B. amylovorus*, and *Endothia*.

9b. *Parenchymal necrosis*, in which chiefly the parenchyma is affected, including the greater number of the soft rots; for example, soft rots caused by *B. carotovorus*, *Rhizopus*, *Penicillium*, *Phythia-cysitis*, *Rhizoctonia*, *Pythium*, *Phytophthora*, *Sclerotinia*, *Botrytis*, *Colletotrichum*, and *Gleosporium*.

9c. *Macular necrosis*, in which necrosis is limited to spots, chiefly occurring on leaves. This is divided into (1) macular necrosis with abscission (the "shothole" diseases caused, for example, by *Cylindrosporium* and *Marssonina*); (2) macular necrosis without abscission (chiefly the leaf spots, caused, for example, by *Pseudopeziza*, *Entomosporium*, *Macrosporium*, *Lophoderma*, *Guignardia* [*Phyllosticta*], *Ascochyta*, *Ramularia*, *Septoria*, *Diplodia*, *Cercospora*, *Colletotrichum*, *Gleosporium*, *Fusicladium*, *Cladosporium*, and *Alternaria*).

The following synopsis may make these categories and their interrelations clear.

I. The parasite living in the sap or in cavities or parts devoid of living protoplasm: (1) embolism; (2) wood rots.

II. The parasite for the major part of its life drawing its nutriment from host cells that are still living: (3) endocellular parasitism; (4) endocellular haustorial parasitism; (5) epidermitis; (6) intercellular mycosis; (7) mycosclerosis; (8) tumor.

III. The parasite living within host cells or tissues which have recently been killed or partially disorganized by it: (9) necrosis; (9a) cortical necrosis; (9b) parenchymal necrosis; (9c) macular necrosis; (9c') macular necrosis with abscission; (9c'') macular necrosis without abscission.

There is an apparent omission of hypertrophy and hyperplasia, but I regard these two manifestations as symptoms rather than as definite diseases.

FLOWERS AND INSECTS. XX

EVOLUTION OF ENTOMOPHILOUS FLOWERS

CHARLES ROBERTSON

In his *Fertilisation of flowers* (pp. 594, 595) MÜLLER arrives at the following conclusions with regard to the development of flowers:

The transition from wind fertilization to insect fertilization, and the first traces of adaptation to insects, could only be due to the influence of quite short-lipped insects with feebly developed color-sense. The most primitive flowers are therefore for the most part (except, for instance, *Salix*) simple, widely open, regular, devoid of honey or with their honey unconcealed and easily accessible, and white or yellow in color (for example, most Umbelliferae and Alsineae, many Ranunculaceae and Rosaceae).

Gradually, from the miscellaneous lot of flower-visiting insects, all much alike in their tastes, there arose others more skilful and intelligent, with longer tongues and acuter color-sense; and they gradually caused the production of flowers with more varied colors, honey invisible to or beyond the reach of the less intelligent short-tongued guests, and various contrivances for lodging, protecting, and pointing out the honey.

The Ichneumonidae at first surpassed all other visitors in observation and discernment, and they were thus able to produce inconspicuous flowers which escaped the notice of other visitors. On the appearance of sand wasps and bees these inconspicuous flowers were banished by competition to the less frequented localities (for example, *Listera* to shady woods).

The sand wasps (Sphegidae) apparently took the place to a great extent of the ichneumons, and produced flowers where organs had to be thrust apart (Papilionaceae), or where a narrow cavity had to be entered (Labiales), or where some other action similar to the act of digging had to be performed. Subsequently bees seem to have entered on joint possession of most of these flowers, and to have added special adaptations of their own.

The true wasps (Vespidae) could establish themselves by the fear of their sting (and of their jaws) in sole possession of certain flowers with wide open mouths and abundant honey. These they developed further in relation to their wants (*Scrophularia*, *Symphoricarpos*, *Epipactis latifolia*, *Lonicera alpi-gena*); but where wasps are scarce the flowers are utilized by other insects.

Bees (Apidae), as the most skilful and diligent visitors, have played the chief part in the evolution of flowers; we owe to them the most numerous, most varied, and most specialized forms.